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Endocrine factors and ovarian follicles are influenced by body condition and somatotropin in postpartum beef cows[1,2]

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ABSTRACT: Multiparous beef (1/4 to 3/8 *Bos indicus*; n = 99) cows were managed to achieve low (BCS = 4.3 ± 0.1; n = 50) or moderate (BCS = 6.1 ± 0.1; n = 49) body condition (BC) to determine the influence of bovine (b) ST on the number of follicles, diameter of largest follicle, and serum concentrations of IGF-I, triiodothyronine (T3), thyroxine (T4), and prolactin. Beginning 32 d postpartum, cows within each BC were assigned randomly to treatment with or without bST. Non-bST-treated cows received no treatment, and treated cows were administered bST (Posilac, 500 mg, s.c.) on d 32, 46, and 60 postpartum. On d 60, all cows received a controlled internal drug-releasing (CIDR) device for 7 d and $PGF_{2\alpha}$ at CIDR removal (CIDR-$PGF_{2\alpha}$). Blood samples (7 mL) were collected at each bST treatment and d 39 and 67 postpartum. Ultrasound was performed 1 d after CIDR-$PGF_{2\alpha}$ to determine the number of small (2 to 9 mm) and large (≥10 mm) follicles and the diameter of largest follicle. Cows treated with bST in low BC had increased ($P < 0.05$) IGF-I vs. low-BC non-bST-treated cows on d 39, 46, 60, and 67 postpartum. Prolactin and T3 were greater ($P < 0.05$) in moderate-BC than in low-BC cows on all sample dates. Thyroxine was greater ($P < 0.001$) in moderate-BC cows on d 46, 60, and 67 compared with low-BC cows. On d 67, bST-treated cows had greater ($P < 0.05$) T4 compared with non-bST-treated cows. Diameter of the largest follicle 1 d after CIDR-$PGF_{2\alpha}$ was greater ($P < 0.01$) in anestrous cows treated with bST than for non-bST-treated anestrous cows. Diameter of the largest follicle was correlated with concentrations of IGF-I ($r \geq 0.18$; $P \leq 0.08$), T3 ($r \geq 0.17$; $P \leq 0.10$), and prolactin ($r \geq 0.20$; $P \leq 0.06$). Treatment with bST increased IGF-I in low-BC cows, and IGF-I was correlated with the diameter of the largest follicle 1 d after CIDR-$PGF_{2\alpha}$. Undernutrition of cattle may be communicated to the hypothalamic-pituitary-ovarian axis via metabolic hormones including IGF-I, thyroid hormones, or prolactin.

Key words: beef cow, body condition, follicle, insulin-like growth factor-I, somatotropin, thyroid hormone

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INTRODUCTION

The nutritional status of cattle is communicated within the hypothalamic-pituitary-ovarian axis via metabolic hormones and (or) blood metabolites (Keisler and Lucy, 1996; Wettemann and Bossis, 2000). Nutrient restriction uncouples the positive relationship of the GH-IGF axis with increased GH and reduced IGF-I (Armstrong et al., 1993; Bossis et al., 1999). Follicular dynamics are influenced by GH and IGF-I (Spicer and Echternkamp, 1995; Lucy, 2000), and beef cattle in low BCS have decreased follicular development compared with cows in adequate BCS (Perry et al., 1991; Bossis et al., 1999). Other blood metabolites and (or) hormones are probably involved in mediating nutritional status (Keisler and Lucy, 1996; Lucy, 2000; Wettemann and Bossis, 2000). A direct effect of thyroid activity on ovarian function of cattle has not been reported; however, induced hyperthyroidism reduced BW and BCS, and increased the incidence of anestrous cows (De Moraes et al., 1998). Concentrations of thyroxine (**T4**) were decreased in nutrient-restricted cows (Richards et al.,

[1]Names are necessary to report factually on available data; however, the USDA does not guarantee or warrant the standard of the product, and the use of the name by the USDA implies no approval of the product to the exclusion of others that also may be suitable.

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1995; Lents et al., 2005). Prolactin has been suggested to influence gonadotropin release in sheep (Tortonese et al., 1998) and mares (Gregory et al., 2000). Prolactin receptors have been found in the bovine corpus luteum (**CL**; Poindexter et al., 1979) and granulosa cells (Lebedeva et al., 2001, 2004). Cows with greater nutrient intake had increased plasma prolactin than cows with lower nutrient intake (Wright et al., 1987).

We recently reported (Flores et al., 2007) that recombinant bovine (b)ST increased GH in beef cattle and hypothesized that bST would alter other metabolic hormones and might influence ovarian follicles in postpartum cows. A better understanding of the effects of body condition (**BC**) and ST on ovarian and endocrine function in beef cattle is warranted.

The objectives were to evaluate the effects of BC and bST on the number of small and large follicles, diameter of the largest follicle, and concentrations of IGF-I, triiodothyronine (**T3**), T4, and prolactin in postpartum beef cows.

MATERIALS AND METHODS

Description of Animals and Experimental Procedures

The committee for animal welfare at the USDA-ARS, Dale Bumpers Small Farms Research Center (Booneville, Arkansas) approved the animal procedures used in this experiment.

Spring-calving, crossbred Angus (1/4 to 3/8 *Bos indicus*; mean age = 3.7 ± 1.3 yr), multiparous cows were managed to achieve a low or moderate BC, as described previously (Flores et al., 2007). Briefly, cows grazed stockpiled and spring-growth, endophyte-infected tall fescue [*Festuca arundinacea* (Schreb), syn. *Lolium arundinaceum* (Schreb.) Darbysh] pastures at a stocking rate of either 1 cow/0.3 ha (low BC) or 1 cow/0.8 ha (moderate BC) for approximately 162 d before the initiation of bST treatment; all cows were maintained on tall fescue pastures during bST treatment. Mean BCS of low- (n = 50; mean BW = 424 ± 11 kg) and moderate- (n = 49; mean BW = 530 ± 11 kg) BC cows was 4.3 ± 0.1 and 6.1 ± 0.1 (1 = emaciated to 9 = obese; Wagner et al., 1988), respectively, at the initiation of bST treatment. Body weight change of the cows during the experiment was not influenced ($P > 0.10$) by bST treatment, BC, or both; all cows gained 0.4 kg/d (Flores et al., 2007). Low-BC cows gained BC (0.3 BCS units) and moderate-BC cows lost ($P < 0.001$) BC (–0.5 BCS units) during the experiment (Flores et al., 2007).

Calving dates for low- and moderate-BC cows ranged from 21 February to 28 March (mean date = 9 March) and 24 February to 2 April (mean date = 14 March), respectively. Calves were allowed to suckle their dams throughout the experiment. Beginning 32 ± 2 d postpartum, cows were randomly assigned to treatment in a 2 × 2 arrangement, with the main effects of bST (0 or 500 mg) and BC (low and moderate). Non-bST-treated cows received no bST treatment, and treated cows were administered bST (500 mg, s.c.; Posilac, St. Louis, MO) on d 32, 46, and 60 postpartum. A similar number of cows was in each treatment group: non-bST-treated low BC (n = 25) non-bST-treated moderate-BC (n = 24), bST-treated low-BC (n = 25), and bST-treated moderate-BC (n = 25). On d 60, all cows received an intravaginal controlled internal drug-releasing [**CIDR**, 1.38 g of progesterone (**P$_4$**); Pfizer Animal Health, New York, NY] device. After 7 d, the CIDR were removed and all cows received PGF$_{2\alpha}$ (25 mg, i.m.; Lutalyse, Pfizer Animal Health).

Ultrasound, Blood Collection, and Hormone Determination

Ultrasonography (Aloka SSD 500-V ultrasound scanner equipped with a 7.5-MHz linear array transrectal transducer, Aloka Co. Ltd., Wallingford, CT) was performed by a single technician without knowledge of the treatments 1 d after CIDR removal and PGF$_{2\alpha}$ (**CIDR-PGF$_{2\alpha}$**) to determine the number of small (2 to 9 mm) and large (≥10 mm) follicles and the diameter of the largest follicle. Blood samples (7 mL) were obtained from the cows at bST treatment (d 32, 46, and 60 postpartum) and on d 39 and 67. Blood samples were collected by venipuncture of the median caudal vein into Vacutainers (Becton Dickinson, Franklin Lakes, NJ), allowed to clot for 24 h at 4°C, and then centrifuged (1,500 × g for 25 min). Serum samples were stored at –20°C until analyses.

Serum concentrations of T3, T4, and P$_4$ were determined in duplicate by solid-phase RIA using components of commercial kits (Siemens Diagnostic, Los Angeles, CA). These kits utilized antibody-coated tube technology, and the assays were performed without prior extraction of the individual hormones from the serum. The T3 and T4 assays were validated in ruminant serum, as described by Wells et al. (2003) and Richards et al. (1999), respectively, and within- and between-assay CV were less than 10% for both thyroid hormones. Validation of the P$_4$ RIA was reported by Schneider and Hallford (1996). In this experiment, intra- and interassay CV for P$_4$ determinations were 5 and 1%, respectively. Serum IGF-I and prolactin concentrations were determined in duplicate by double-antibody RIA, as described by Berrie et al. (1995) and Spoon and Hallford (1989), respectively, using primary antisera and purified standard and iodination preparations supplied by the National Hormone and Peptide Program (Torrance, CA). Assay of total serum IGF-I was conducted after acid-ethanol inactivation of binding proteins and resulted in intra- and interassay CV of 12 and 16%, respectively. Serum prolactin was quantified in a single assay, which had a CV of 7%.

Serum samples collected on d 32, 39, and 46 postpartum were analyzed for concentrations of P$_4$ to determine luteal status at the initiation of bST treatment. Cows were classified as anestrous if the concentrations of P$_4$

were <1 ng/mL in the weekly blood samples or cyclic if the concentrations of P_4 were ≥1 ng/mL in at least 1 blood sample (Wettemann et al., 1972).

Statistical Analyses

Data were analyzed by ANOVA as a 2 × 2 × 2 factorial arrangement of treatments (low or moderate BC, bST or no bST treatment, and anestrous or cyclic) within a completely randomized design, with cow as the experimental unit. The number of small and large follicles and the diameter of the largest follicle were analyzed by ANOVA utilizing the GLM procedure (SAS Inst. Inc., Cary, NC). The model included bST treatment, BC, luteal status at the initiation of bST treatment, and the interactions. Comparisons of concentrations of IGF-I, T3, T4, and prolactin were analyzed using the MIXED procedure of SAS for repeated measures (Littell et al., 1998). The model included bST treatment, BC, luteal status at the initiation of bST treatment, day, and all interactions. The most appropriate covariance structure for each analysis was chosen from unstructured, compound symmetric, spatial power, and ante-dependence structures utilizing Akaike's information criterion and Schwarz' Bayesian criterion (Littell et al., 2000). Kenward-Rogers' approximation was used for calculation of the degrees of freedom of the pooled error term. The random effect of cow within each BC, bST treatment, and luteal status (specified in the SUBJECT statement) accounted for the correlations among repeated observations on the same cow. If the interaction of bST treatment × day, BC × day, or bST treatment × BC × day was significant ($P < 0.05$), means separations were evaluated on each day using the PDIFF function of SAS. Days postpartum were different between low- and moderate-BC cows at the initiation of the bST treatment (Flores et al., 2007); therefore, day postpartum was used as a covariate in all of the aforementioned models. However, day postpartum was not significant ($P > 0.10$) in any of the models. Pearson correlations were generated with the CORR procedure of SAS to evaluate the relationships between concentrations of hormones and the diameter of the largest follicle 1 d after CIDR-$PGF_{2\alpha}$.

RESULTS

Seventy-eight percent (77/99) of cows in the current experiment were anestrous at the initiation of bST treatment; the number of anestrous cows was similar between bST treatment ($P = 0.36$), BC ($P = 0.91$), and bST treatment × BC ($P = 0.58$). Diameter of the largest follicle 1 d following CIDR-$PGF_{2\alpha}$ was influenced ($P = 0.01$) by a bST treatment × luteal status interaction. Diameter of the largest follicle was greater ($P < 0.05$) in anestrous cows treated with bST than for non-bST-treated anestrous cows; non-bST-treated cyclic cows had greater ($P < 0.05$) diameter of the largest follicle compared with non-bST-treated anestrous cows (Figure 1A). Diameter of the largest follicle 1 d following CIDR-$PGF_{2\alpha}$ was influenced ($P = 0.03$) by a bST treatment × BC interaction. Diameter of the largest follicle was greatest ($P < 0.05$) for non-bST-treated moderate-BC cows compared with other treatment groups (Figure 1B). The number of small follicles 1 d following CIDR-$PGF_{2\alpha}$ was influenced ($P = 0.02$) by a bST treatment × BC interaction. The number of small follicles was greater ($P < 0.05$) in non-bST-treated low-BC cows compared with other treatment groups (Figure 2). The number of large follicles 1 d following CIDR-$PGF_{2\alpha}$ was not influenced ($P > 0.10$) by bST treatment, BC, or luteal status at initiation of bST treatment or the interactions. Mean number of large follicles was 1.7 ± 0.2.

Serum concentrations of IGF-I were influenced ($P < 0.001$) by a bST treatment × BC × day interaction (Figure 3). On d 39, 46, 60, and 67 postpartum, bST-treated moderate-BC cows had greater ($P < 0.05$) concentrations of IGF-I compared with bST-treated low-BC, non-bST-treated moderate-BC, and non-bST-treated low-BC cows (Figure 3). However, bST-treated low-BC cows had greater ($P < 0.05$) concentrations of IGF-I than non-bST-treated low-BC cows on d 39, 46, 60, and 67. A BC × luteal status interaction influenced ($P = 0.01$) serum concentrations of IGF-I. Anestrous and cyclic cows in moderate BC had increased ($P < 0.05$) serum IGF-I than anestrous and cyclic cows in low BC; cyclic cows in low BC had greater ($P < 0.05$) concentrations of IGF-I compared with anestrous cows in low BC (Figure 4). Serum concentrations of IGF-I at d 39 ($r = 0.18$; $P = 0.08$), 60 ($r = 0.22$; $P = 0.03$), and 67 ($r = 0.19$; $P = 0.07$) were positively correlated with the diameter of the largest follicle 1 d following CIDR-$PGF_{2\alpha}$.

Serum concentrations of T3 were influenced by a BC × day ($P < 0.001$) interaction. On all sample dates, moderate-BC cows had greater ($P < 0.05$) concentrations of T3 compared with low-BC cows (Figure 5A). Concentrations of T3 were affected ($P = 0.02$) by a bST treatment × BC × luteal status interaction. Cyclic cows with or without bST treatment in low or moderate BC had increased ($P < 0.05$) T3 compared with other treatment groups (data not shown). Concentrations of T3 on d 32 ($r = 0.24$; $P = 0.02$), 39 ($r = 0.18$; $P = 0.09$), 46 ($r = 0.25$; $P = 0.01$), 60 ($r = 0.17$; $P = 0.10$), and 67 ($r = 0.23$; $P = 0.03$) were positively correlated with diameter of the largest follicle 1 d following CIDR-$PGF_{2\alpha}$.

Serum concentrations of T4 were influenced by a BC × day ($P = 0.001$) and bST treatment × day ($P = 0.001$) interaction. Concentrations of T4 were greater ($P < 0.05$) in moderate-BC cows on d 46, 60, and 67 postpartum compared with low-BC cows (Figure 5B). On d 67, bST-treated cows (45.9 ± 1.1 ng/mL) had increased ($P < 0.05$) concentrations of T4 compared with non-bST-treated cows (42.2 ± 1.4 ng/mL). Luteal status influenced ($P = 0.01$) concentrations of T4 such that cyclic cows (43.8 ± 1.3 ng/mL) had greater ($P < 0.05$) serum concentrations of T4 than anestrous cows (39.6 ± 0.7 ng/mL). Unlike concentrations of T3, concentrations of T4 were not ($P > 0.10$) correlated with the diameter

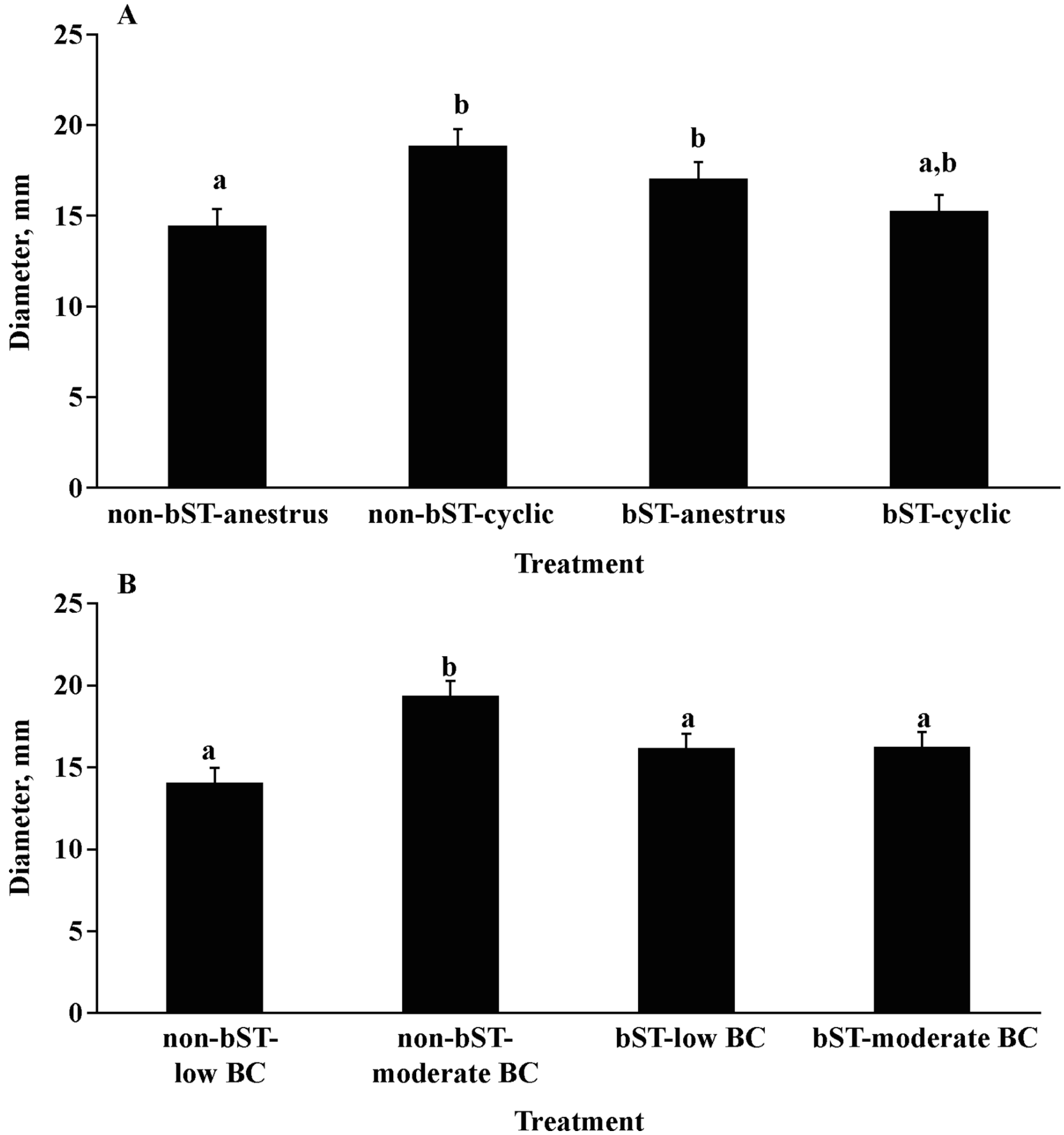

Figure 1. Diameter of the largest follicle of anestrous (concentrations of progesterone <1 ng/mL on d 32, 39, and 46 postpartum) and cyclic (concentrations of progesterone ≥1 ng/mL in at least 1 blood sample on d 32, 39, and 46 postpartum) beef cows in low- (BCS = 4.3 ± 0.1) and moderate- (BCS = 6.1 ± 0.1) body condition (BC) and treated with bovine (b) ST or without bST (non-bST). Treated cows were administered bST every 2 wk for 6 wk beginning 32 d postpartum. All cows received an intravaginal controlled internal drug-releasing (CIDR) device containing progesterone for 7 d; $PGF_{2\alpha}$ was administered at the time of CIDR removal. Ultrasonography was performed 1 d after CIDR removal and $PGF_{2\alpha}$ to determine the diameter of the largest follicle. Diameter of the largest follicle was influenced by a bST treatment × luteal status (anestrous or cyclic) interaction (A; $P = 0.01$) and a bST treatment × BC interaction (B; $P = 0.03$). [a,b]Means without common letters differ ($P < 0.05$).

of the largest follicle 1 d following CIDR-$PGF_{2\alpha}$ (data not shown).

As with concentrations of thyroid hormones, serum concentrations of prolactin were influenced by a BC × day interaction ($P < 0.001$). On all sample dates, moderate-BC cows had greater ($P < 0.05$) concentrations of prolactin compared with low-BC cows (Figure 5C). Treatment with bST did not affect ($P = 0.48$) concentrations of prolactin; however, luteal status influenced ($P = 0.03$) concentrations of prolactin. Cyclic cows (18.4 ± 2.9 ng/mL) had greater ($P < 0.05$) serum concentrations of prolactin compared with anestrous cows (11.4 ± 1.5 ng/mL). Similar to concentrations of T3, concentrations of prolactin on d 32 (r = 0.28; $P = 0.01$), d 39 (r = 0.25; $P = 0.02$), 46 (r = 0.29; $P = 0.01$), 60 (r = 0.28; $P = 0.01$), and 67 (r = 0.20; $P = 0.06$) were positively correlated with the diameter of the largest follicle 1 d following CIDR-$PGF_{2\alpha}$.

DISCUSSION

Reduced reproductive performance in cattle due to low body energy reserves is well established (Short et

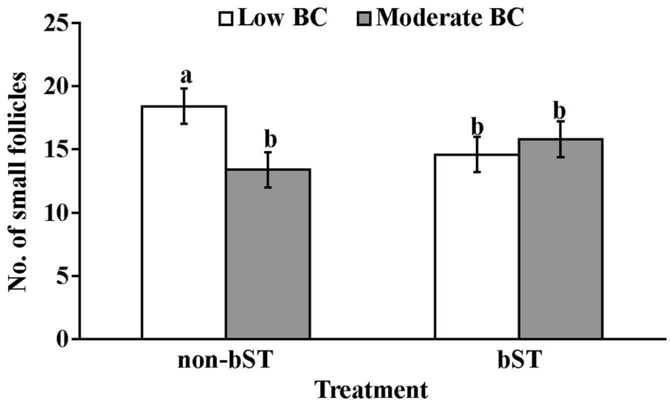

Figure 2. Number of small follicles (2 to 9 mm) of low- (BCS = 4.3 ± 0.1) and moderate- (BCS = 6.1 ± 0.1) body condition (BC) beef cows treated with bovine (b) ST or without bST (non-bST). Cows were administered bST every 2 wk for 6 wk beginning 32 d postpartum. All cows received an intravaginal controlled internal drug-releasing (CIDR) device containing progesterone for 7 d; $PGF_{2\alpha}$ was administered at the time of CIDR removal. Ultrasonography was performed 1 d after CIDR removal and $PGF_{2\alpha}$ to determine the number of small follicles. The number of small follicles was influenced ($P = 0.02$) by a bST treatment × BC interaction. [a,b]Means without common letters differ ($P < 0.05$).

al., 1990; Diskin et al., 2003; Wettemann et al., 2003); however, minimal research exists on the relationship between BC, ST, and their interactions on follicular and endocrine function of beef cattle. Luteal status (anestrous or cyclic) of cows influences follicular responses to synchronization protocols (Stevenson et al., 2003; Saldarriaga et al., 2007). To achieve our objectives of evaluating BC and bST on follicular and endocrine function, a majority (78%) of cows in the current experiment were anestrous at the initiation of bST treatment. Diameter of the largest follicle 1 d following CIDR-$PGF_{2\alpha}$ was greater in bST-treated anestrous cows than for non-bST-treated anestrous cows. Nutrient restriction and subsequent BC losses resulted in smaller dominant follicles in beef heifers (Rhodes et al., 1995; Bossis et al., 1999) as well as beef (Ciccioli et al., 2003) and dairy (Lucy et al., 1991) cows. Britt (1992) projected that 60 to 80 d is needed for a bovine follicle to grow from an early preantral stage to a mature stage ready for ovulation, and follicles exposed to adverse conditions (i.e., negative energy balance) during growth could result in impaired development. Anestrous cows not treated with bST had decreased diameter of the largest follicle after CIDR removal and $PGF_{2\alpha}$ in the current experiment. However, treatment of anestrous cows with bST every 2 wk for 6 wk resulted in similar diameters of the largest follicle among anestrous bST-treated cows and cyclic cows with or without bST.

The exact mechanisms of how bST affects ovarian function in cattle are unclear. Increased follicular growth in anestrous cattle treated with exogenous bST in the current experiment probably cannot be attributed to alterations in gonadotropin release, because several studies have suggested decreases in concentrations of gonadotropins in dairy cows treated with exogenous bST (Waterman et al., 1993; Kirby et al., 1997). Plasma LH and FSH and their receptors in the ovary were not altered by bST treatment in beef heifers (Gong et al., 1991) or beef cows (Andrade et al., 1996). We recently reported that bST increased concentrations of GH in beef cows (Flores et al., 2007). Effects of GH on ovarian function may be direct because ST receptors are found in numerous reproductive tissues of cattle (Lucy et al., 1993; Kirby et al., 1996) including the CL. Effects of ST also can be indirect through its mediator of biological action, IGF-I. Type I IGF receptor mRNA has been detected in bovine preantral follicles (Armstrong et al., 2002), and postpartum treatment of low- and moderate-BC cows with bST increased concentrations of IGF-I in the current experiment. Plasma IGF-I was greater in dairy cows treated with exogenous ST than in control cows (Bilby et al., 1999). Nutrient restriction uncouples the positive relationship of the GH-IGF axis with increased concentrations of GH and reduced IGF-I (Butler et al., 2003). Insulin-like growth factor-I along with gonadotropins are important to the growth and differentiation of follicles (Spicer and Echternkamp, 1995). Slot et al. (2006) recently reported treatment of female GH-receptor knockout mice with IGF-I for 14 d resulted in an increase in the number of healthy antral follicles and a decrease in the percentage of atretic follicles. Somatotropin treatment increased concentrations of IGF-I in postpartum cows in the current experiment and is at least partly responsible for the increase in diameter of the largest follicle in anestrous cows.

Serum concentrations of IGF-I were positively correlated with the diameter of the largest follicle in the current experiment. Reduced concentrations of IGF-I in Brahman cattle with a GH-receptor deficiency was associated with fewer small (2 to 5 mm) follicles and cessation of growth of the dominant follicle after d 5 of the estrous cycle (Chase et al., 1998). Armstrong and Benoit (1996) reported decreased plasma IGF-I due to diminished GH receptor activity in nutrient-restricted cows. Non-bST-treated cows in low BC had reduced concentrations of IGF-I in the current experiment; however, bST treatment of low-BC cows increased IGF-I. The increase in serum IGF-I in low-BC cows treated with bST was less than the increase in IGF-I in moderate-BC cows treated with bST. Reduced IGF-I responsiveness in nutrient-restricted cattle has been attributed to decreased hepatic binding of GH (Breier et al., 1988). Reduced concentrations of IGF-I were associated with decreased size of the ovulatory follicle and CL in nutrient-restricted beef heifers (Bossis et al., 1999). Beyond the scope of the current experiment, the role of IGF-I on the ovary also can be influenced by IGFBP that increase the half-life of IGF in circulation and may

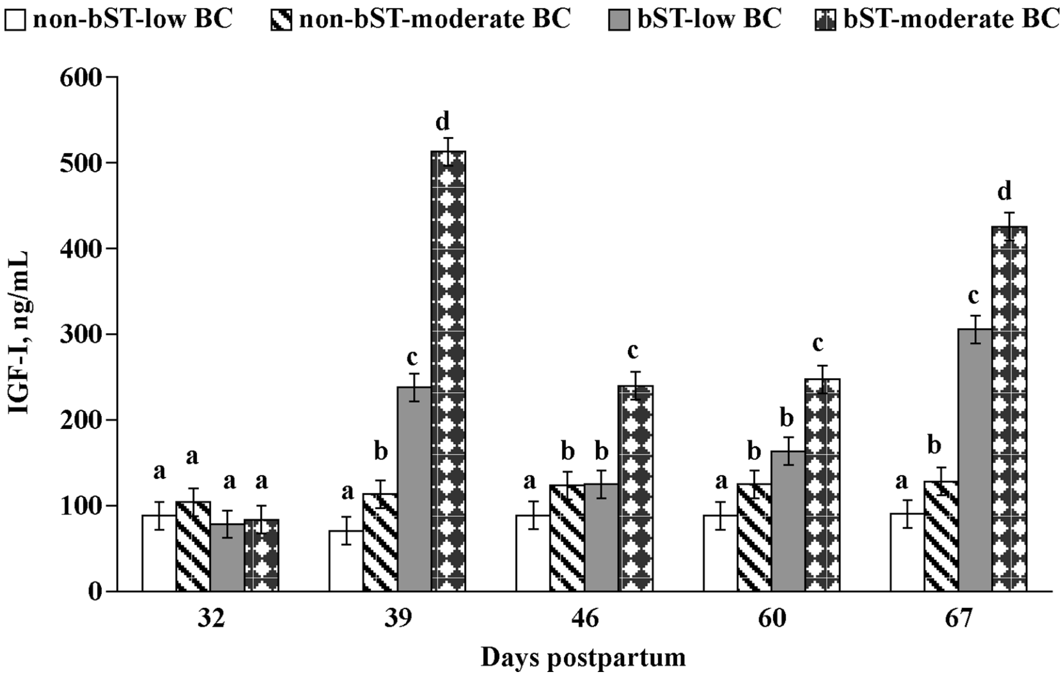

Figure 3. Serum concentrations of IGF-I of low- (BCS = 4.3 ± 0.1) and moderate- (BCS = 6.1 ± 0.1) body condition (BC) beef cows treated with bovine (b) ST or without bST (non-bST). Cows were administered bST every 2 wk for 6 wk beginning 32 d postpartum. Blood (7 mL) was collected at each bST treatment (d 32, 46, and 60 postpartum) and on d 39 and 67. Insulin-like growth factor-I was influenced ($P < 0.001$) by a bST treatment × BC × day interaction. [a-d]Within a day, means without common letters differ ($P < 0.05$).

either increase or decrease the bioavailability of IGF (Roberts et al., 1997). Llewellyn et al. (2007) suggested that reduced expression of IGFBP-2 mRNA in thin dairy cows influenced the bioavailability of circulating IGF-I possibly altering the prerecruitment of ovarian follicles required to sustain normal postpartum ovarian function. In the current experiment, anestrous cows in low BC had decreased serum IGF-I; however, bST treatment of anestrous cows increased the diameter of the largest follicle compared with non-bST-treated anestrous cows. We speculate that exogenous bST resulted in adequate serum IGF-I during early follicular development culminating in increased diameter of the largest follicle in anestrous cows.

The number of small follicles following CIDR removal and $PGF_{2\alpha}$ was increased in non-bST-treated low-BC cows. In dairy cattle, exogenous bST influences follicular growth differently depending on size of the follicle. Daily treatment with bST (25 mg) for 19 d increased the number of 6- to 15-mm follicles in lactating cows (De La Sota et al., 1993). The number of small to medium (3 to 9 mm) follicles in Holstein cows was not influenced by bST treatment (500 mg) administered every 14 d for 42 d; however, bST did increase the number of follicles ≥10 mm (Kirby et al., 1997). Gong et al. (1991) reported that the number of small (2 to 5 mm), but not medium (5 to 10 mm) or large (>10 mm) follicles was increased in Hereford × Friesian heifers administered bST (25 mg) daily. Less is known of the effects of ST on follicular dynamics in beef cattle. A single administration (320 mg) of bST increased the number of small follicles (<5 mm) but did not affect the number of medium (5 to 9 mm) or large (>9 mm) follicles in synchronized Nelore (*Bos indicus*) heifers (Buratini et al., 2000). Andrade et al. (1996) found that follicle populations did not differ between postpartum beef cows administered bST (320 mg) every 2 wk for 8 wk and control cows. Differences between dosage and duration of bST administration among studies would obviously contribute to varying results. Further, the number of small follicles is extremely variable among individual animals (Erickson, 1966) and may affect how bST influences follicle numbers. Treatment of low-BC cows with bST resulted in similar numbers of small follicles among bST-treated low-BC cows and moderate-BC cows with or without bST treatment.

Concentrations of T3 and T4 were greater in moderate-BC cows than low-BC cows. Triiodothyronine is the metabolically active thyroid hormone (Leonard and Visser, 1986), and T4 is converted to active T3 in the thyroid gland and other tissues by 5′-deiodinase (Leonard and Visser, 1986; Chanoine et al., 1993). Induced hyperthyroidism increased serum T3, which reduced BW and BCS in Brahman cows and increased the number of anestrous cows, suggesting that the influence of thyroid hormones on cattle reproduction may be indirect via loss of adequate body energy reserves (De Moraes et al., 1998). Concentrations of T4 were decreased in nutrient-restricted cows (Richards et al., 1995; Capuco et al., 2001), and cows with increased nutrient intake had

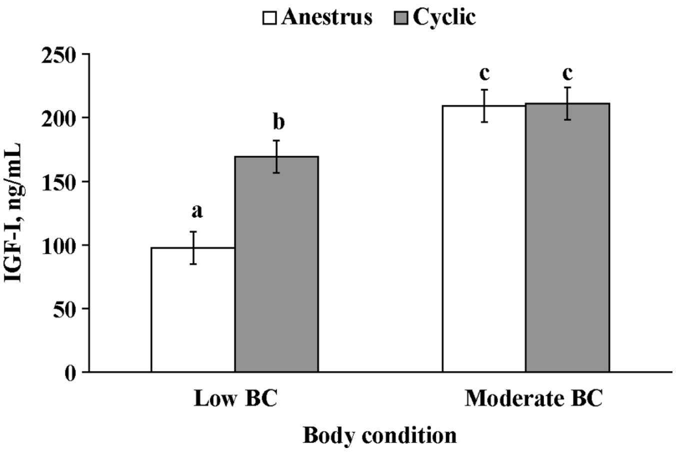

Figure 4. Serum concentrations of IGF-I of anestrous (concentrations of progesterone <1 ng/mL on d 32, 39, and 46 postpartum) and cyclic (concentrations of progesterone ≥1 ng/mL in at least 1 blood sample on d 32, 39, and 46 postpartum) beef cows in low (BCS = 4.3 ± 0.1) or moderate (BCS = 6.1 ± 0.1) body condition (BC). Insulin-like growth factor-I was influenced (P = 0.01) by a BC × luteal status (anestrous or cyclic) interaction. [a-c]Means without common letters differ (P < 0.05).

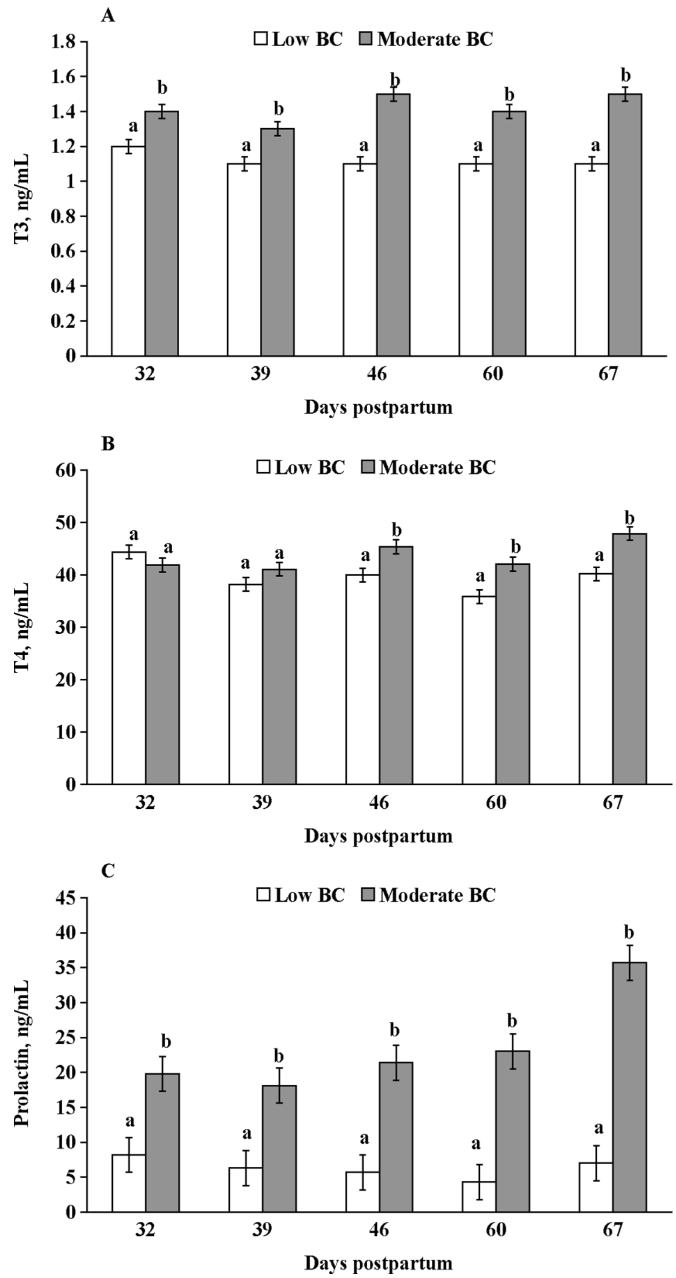

Figure 5. Serum concentrations of triiodothyronine (T3; A), thyroxine (T4; B), and prolactin (C) of low- (BCS = 4.3 ± 0.1) and moderate- (BCS = 6.1 ± 0.1) body condition (BC) beef cows treated with bovine (b) ST or without bST. Cows were administered bST every 2 wk for 6 wk beginning 32 d postpartum. Blood (7 mL) was collected at each bST treatment (d 32, 46, and 60 postpartum) and on d 39 and 67. All hormones were influenced (P < 0.001) by a BC × day interaction. [a,b]Within a day, means without common letters differ (P < 0.05).

greater concentrations of T4 (Lents et al., 2005). Direct effects of thyroid hormones on ovarian function are unclear. Induced hypothyroidism increased ovarian weights and the number of large (≥8 mm) follicles in superovulated Brahman cows but reduced embryo recovery and fertilization rate (Bernal et al., 1999). Spicer et al. (2001) reported direct stimulatory effects of T3 and T4 on thecal cell steroidogenesis in vitro, which may result in increased estrogen production by the follicle. Concentrations of T3 were positively correlated with diameter of the largest follicle 1 d following CIDR-$PGF_{2\alpha}$ in the current experiment. Further, anestrous cows in low BC had reduced concentrations of T4, which was associated with a smaller dominant follicle. Serum thyroid hormones were altered by BC and may mediate effects of nutrition on the ovary in beef cattle.

Cows treated with bST had increased concentrations of T4 on d 67. Similarly, treatment of Holstein cows with bST (40 mg/d) for 6 d increased serum concentrations of T4 by 12% compared with control cows, but did not influence serum concentrations of T3 (Capuco et al., 2001). Continuous infusion of bST (29 mg/d) for 63 d reduced 5′-deiodinase in the liver but not mammary gland tissue of dairy cows, establishing a metabolic preference for the mammary gland (Kahl et al., 1995). Increased T4 after bST treatment may be an indication of lipolysis, which is a major activity of ST (Bauman, 1999), and treatment with bST increased concentrations of NEFA in beef cows (Flores et al., 2007). Increased thyroid hormones following bST treatment suggest that ST alters the metabolic status of the animal; however, the current bST treatment protocol did not alter BW or BCS of cows during the current experiment (Flores et al., 2007).

Similar to concentrations of thyroid hormones, concentrations of prolactin were greater in moderate-BC cows compared with low-BC cows. Further, prolactin was reduced in anestrous cows, but not affected by bST treatment. Cows with greater BC had increased plasma prolactin than thin beef cows (Wright et al., 1987). Prolactin is important for the maintenance and secretory activity of the CL in rodents (Morishige and Rothchild, 1974) and prolactin influences gonadotropin release in sheep (Tortonese et al., 1998) and mares (Gregory et al., 2000). Less is known of prolactin effects on follicular dynamics in beef cattle and results have been inconsistent. Prolactin receptors have been reported in the bovine CL (Poindexter et al., 1979) and granulosa cells (Lebedeva et al., 2001, 2004). Follicular fluid concentrations of prolactin increased as follicle size increased (Henderson et al., 1982). However, Wise and Maurer (1994) reported that follicular prolactin decreased with follicle size in beef heifers, and follicular prolactin and progesterone were inversely related. Concentrations of prolactin were greater in the follicular fluid of normal, nonatretic follicles compared with atretic follicles (Lebedeva et al., 1998). Estrogens stimulate synthesis of pituitary prolactin (Jordan and Koch, 1989), and follicular prolactin paralleled follicular estrogen after $PGF_{2\alpha}$ administration in beef heifers (Wise and Maurer, 1994). Concentrations of prolactin were influenced by BC and luteal status of cows in the current experiment. It is possible that prolactin may convey the nutritional status of the cow to the hypothalamus and (or) the ovary; however, more research is needed to determine a definite role for prolactin in cow reproduction.

Serum prolactin was correlated with the diameter of the largest follicle 1 d following CIDR-$PGF_{2\alpha}$ in the current experiment. Although concentrations of estrogens were not measured in the current experiment, it is possible that greater concentrations of estrogen from larger follicles may have increased serum prolactin. It has become increasingly evident that either peripheral or follicular prolactin, or both, may play a role in folliculogenesis (Borromeo et al., 1998; Lebedeva et al., 1998, 2001, 2004). Recently, Shibaya et al. (2006) suggested the bovine CL was an extrapituitary site of prolactin production. In the current experiment, prolactin was greater in moderate-BC cows and positively related to the size of the largest follicle and may help communicate the nutritional status of the animal to the hypothalamus and (or) the ovary.

Anestrous cows had smaller dominant follicles 1 d following CIDR-$PGF_{2\alpha}$, and cows in low BC had decreased serum concentrations of IGF-I, T3, T4, and prolactin. Postpartum ST treatment increased the size of the dominant follicle in anestrous cows and increased serum concentrations of IGF-I and T4 in low-BC beef cows. Serum IGF-I, T3, and prolactin were positively related to the size of the dominant follicle. Undernutrition of cattle may be communicated to the hypothalamic-pituitary-ovarian axis via metabolic hormones that include IGF-I, T3, and (or) prolactin. Additional research is needed to determine how serum concentrations of IGF-I, thyroid hormones, and prolactin may be used to enhance reproductive efficiency in anestrous and (or) thin postpartum beef cows.

LITERATURE CITED

Andrade, L. P., S. M. Rhind, I. A. Wright, S. R. McMillen, P. J. Goddard, and T. A. Bramley. 1996. Effects of bovine somatotrophin (bST) on ovarian function in post-partum beef cows. Reprod. Fertil. Dev. 8:951–960.

Armstrong, D. G., G. Baxter, C. O. Hogg, and K. J. Woad. 2002. Insulin-like growth factor (IGF) system in the oocyte and somatic cells of bovine preantral follicles. Reproduction 123:789–797.

Armstrong, J. D., and A. M. Benoit. 1996. Paracrine, autocrine, and endocrine factors that mediate the influence of nutrition on reproduction in cattle and swine: An in vivo, IGF-I perspective. J. Anim. Sci. 74(Suppl. 3):18–35.

Armstrong, J. D., W. S. Cohick, R. W. Harvey, E. P. Heimer, and R. M. Campbell. 1993. Effect of feed restriction on serum somatotropin, insulin-like growth factor-I-(IGF-I) and IGF binding proteins in cyclic heifers actively immunized against growth hormone releasing factor. Domest. Anim. Endocrinol. 10:315–324.

Bauman, D. E. 1999. Bovine somatotropin and lactation: From basic science to commercial application. Domest. Anim. Endocrinol. 17:101–116.

Bernal, A., G. V. DeMoraes, T. A. Thrift, C. C. Willard, and R. D. Randel. 1999. Effects of induced hypothyroidism on ovarian response to superovulation in Brahman (*Bos indicus*) cows. J. Anim. Sci. 77:2749–2756.

Berrie, R. A., D. M. Hallford, and M. L. Galyean. 1995. Effects of zinc source and level on performance, carcass characteristics, and metabolic hormone concentrations of growing and finishing lambs. Prof. Anim. Sci. 11:149–156.

Bilby, C. R., J. F. Bader, B. E. Salfen, R. S. Youngquist, C. N. Murphy, H. A. Garverick, B. A. Crooker, and M. C. Lucy. 1999. Plasma GH, IGF-I, and conception rate in cattle treated with low doses of recombinant bovine GH. Theriogenology 51:1285–1296.

Borromeo, V., A. Berrini, S. Bramani, G. Sironi, M. Finazzi, and C. Secchi. 1998. Plasma levels of GH and PRL and concentrations in the fluids of bovine ovarian cysts and follicles. Theriogenology 49:1377–1387.

Bossis, I., R. P. Wettemann, S. D. Welty, J. A. Vizcarra, L. J. Spicer, and M. G. Diskin. 1999. Nutritionally induced anovulation in beef heifers: Ovarian and endocrine function preceding cessation of ovulation. J. Anim. Sci. 77:1536–1546.

Breier, B. H., P. D. Gluckman, and J. J. Bass. 1988. The somatotrophic axis in young steers: Influence of nutritional status and oestradiol-17 beta on hepatic high- and low-affinity somatotrophic binding sites. J. Endocrinol. 116:169–177.

Britt, J. H. 1992. Impacts of early postpartum metabolism on follicular development and fertility. Bovine Pract. 24:39–43.

Buratini, J., Jr., C. A. Price, J. A. Visintin, and G. A. Bó. 2000. Effects of dominant follicle aspiration and treatment with recombinant bovine somatotropin (BST) on ovarian follicular development in Nelore (*Bos indicus*) heifers. Theriogenology 54:421–431.

Butler, S. T., A. L. Marr, S. H. Pelton, R. P. Radcliff, M. C. Lucy, and W. R. Butler. 2003. Insulin restores GH responsiveness during lactation-induced negative energy balance in dairy cattle: Effects on expression of IGF-I and GH receptor 1A. J. Endocrinol. 176:205–217.

Capuco, A. V., D. L. Wood, T. H. Elsasser, S. Kahl, R. A. Erdman, C. P. Van Tassell, A. Lefcourt, and L. S. Piperova. 2001. Effect of somatotropin on thyroid hormones and cytokines in lactating dairy cows during ad libitum and restricted feed intake. J. Dairy Sci. 84:2430–2439.

Chanoine, J. P., L. E. Braverman, A. P. Farwell, M. Safran, S. Alex, S. Dubord, and J. L. Leonard. 1993. The thyroid gland is a major source of circulating T3 in the rat. J. Clin. Invest. 91:2709–2713.

Chase, C. C., Jr., C. J. Kirby, A. C. Hammond, T. A. Olson, and M. C. Lucy. 1998. Patterns of ovarian growth and development in cattle with a growth hormone receptor deficiency. J. Anim. Sci. 76:212–219.

Ciccioli, N. H., R. P. Wettemann, L. J. Spicer, C. A. Lents, F. J. White, and D. H. Keisler. 2003. Influence of body condition at calving and postpartum nutrition on endocrine function and reproductive performance of primiparous beef cows. J. Anim. Sci. 81:3107–3120.

De La Sota, R. L., M. C. Lucy, C. R. Staples, and W. W. Thatcher. 1993. Effects of recombinant bovine somatotropin (sometribove) on ovarian function in lactating and nonlactating dairy cows. J. Dairy Sci. 76:1002–1013.

De Moraes, G. V., H. R. Vera-Avila, A. W. Lewis, J. W. Koch, D. A. Neuendorff, D. M. Hallford, J. J. Reeves, and R. D. Randel. 1998. Influence of hypo- or hyperthyroidism on ovarian function in Brahman cows. J. Anim. Sci. 76:871–879.

Diskin, M. G., D. R. Mackey, J. F. Roche, and J. M. Sreenan. 2003. Effects of nutrition and metabolic status on circulating hormones and ovarian follicle development in cattle. Anim. Reprod. Sci. 78:345–370.

Erickson, B. H. 1966. Development and radio-response of the prenatal bovine ovary. J. Reprod. Fertil. 11:97–105.

Flores, R., M. L. Looper, R. W. Rorie, M. A. Lamb, S. T. Reiter, D. M. Hallford, D. L. Kreider, and C. F. Rosenkrans Jr. 2007. Influence of body condition and bovine somatotropin on estrous behavior, reproductive performance, and concentrations of serum somatotropin and plasma fatty acids in postpartum Brahman-influenced cows. J. Anim. Sci. 85:1318–1329.

Gong, J. G., T. Bramley, and R. Webb. 1991. The effect of recombinant bovine somatotropin on ovarian function in heifers: Follicular populations and peripheral hormones. Biol. Reprod. 45:941–949.

Gregory, S. J., J. Brooks, A. S. McNeilly, P. M. Ingleton, and D. J. Tortonese. 2000. Gonadotroph-lactotroph associations and expression of prolactin receptors in the equine pituitary gland throughout the seasonal reproductive cycle. J. Reprod. Fertil. 119:223–231.

Henderson, K. M., A. S. McNeilly, and I. A. Swanston. 1982. Gonadotrophin and steroid concentrations in bovine follicular fluid and their relationship to follicle size. J. Reprod. Fertil. 65:467–473.

Jordan, V. C., and R. Koch. 1989. Regulation of prolactin synthesis in vitro by estrogenic and antiestrogenic derivatives of estradiol and estrone. Endocrinology 124:1717–1726.

Kahl, S., A. V. Capuco, M. Binelli, W. K. Vanderkooi, H. A. Tucker, and W. M. Moseley. 1995. Comparison of growth hormone-releasing factor and somatotropin: Thyroid status of lactating, primiparous cows. J. Dairy Sci. 78:2150–2158.

Keisler, D. H., and M. C. Lucy. 1996. Perception and interpretation of the effects of undernutrition on reproduction. J. Anim. Sci. 74(Suppl. 3):1–17.

Kirby, C. J., W. W. Thatcher, R. J. Collier, F. A. Simmen, and M. C. Lucy. 1996. Effects of growth hormone and pregnancy on expression of growth hormone receptor, insulin-like growth factor-I and insulin-like growth factor binding protein-2 and -3 genes in bovine uterus, ovary and oviduct. Biol. Reprod. 55:996–1002.

Kirby, C. J., S. J. Wilson, and M. C. Lucy. 1997. Response of dairy cows treated with bovine somatotropin to a luteolytic dose of prostaglandin $F_{2\alpha}$. J. Dairy Sci. 80:286–294.

Lebedeva, I. Y., V. Y. Denisenko, V. A. Lebedev, and T. I. Kuzmina. 1998. Prolactin in follicular fluid and intracellular store calcium in follicular cells are related to morphological signs of ovarian follicle atresia in cows: Work in progress. Theriogenology 49:509–519.

Lebedeva, I. Y., V. A. Lebedev, and T. I. Kuzmina. 2001. Characterization of somatotropin- and prolactin-binding sites on bovine granulosa cells using homologous hormones. Biochem. (Moscow) 66:967–972.

Lebedeva, I. Y., V. A. Lebedev, and T. I. Kuzmina. 2004. Prolactin and somatotropin binding by granulosa cells of cows at their different reproductive states. Russ. J. Dev. Biol. 35:375–379.

Lents, C. A., R. P. Wettemann, F. J. White, I. Rubio, N. H. Ciccioli, L. J. Spicer, D. H. Keisler, and M. E. Payton. 2005. Influence of nutrient intake and body fat on concentrations of insulin-like growth factor-I, insulin, thyroxine, and leptin in plasma of gestating beef cows. J. Anim. Sci. 83:586–596.

Leonard, J. L., and T. J. Visser. 1986. Biochemistry of deiodination. Pages 189–229 in Thyroid Hormone Metabolism. G. Hennemann, ed. Marcel Dekker, New York, NY.

Littell, R. C., P. R. Henry, and C. B. Ammerman. 1998. Statistical analysis of repeated measures data using SAS procedures. J. Anim. Sci. 76:1216–1231.

Littell, R. C., J. Pendergast, and R. Natarajan. 2000. Modelling covariance structure in the analysis of repeated measures data. Stat. Med. 19:1793–1819.

Llewellyn, S., R. Fitzpatrick, D. A. Kenny, J. J. Murphy, R. J. Scaramuzzi, and D. C. Wathes. 2007. Effect of negative energy balance on the insulin-like growth factor system in pre-recruitment ovarian follicles of post partum dairy cows. Reproduction 133:627–639.

Lucy, M. C. 2000. Regulation of ovarian follicular growth by somatotropin and insulin-like growth factors in cattle. J. Dairy Sci. 83:1635–1647.

Lucy, M. C., J. Beck, C. R. Staples, H. H. Head, R. L. De La Sota, and W. W. Thatcher. 1991. Follicular dynamics, plasma metabolites, and growth factors in lactating cows with positive or negative energy balance during the periestrual period. Reprod. Nutr. Dev. 32:331–341.

Lucy, M. C., R. J. Collier, M. L. Kitchell, J. J. Dibner, S. D. Hauser, and G. G. Krivi. 1993. Immunohistochemical and nucleic acid analysis of somatotropin receptor populations in the bovine ovary. Biol. Reprod. 48:1219–1227.

Morishige, W. K., and I. Rothchild. 1974. Temporal aspects of the regulation of corpus luteum function by luteinizing hormone, prolactin and placental luteotrophin during the first half of pregnancy in the rat. Endocrinology 95:260–274.

Perry, R. C., L. R. Corah, R. C. Cochran, W. E. Beal, J. S. Stevenson, J. E. Minton, D. D. Simms, and J. R. Brethour. 1991. Influence of dietary energy on follicular development, serum gonadotrophins, and first postpartum ovulation in suckled beef cows. J. Anim. Sci. 69:3762–3773.

Poindexter, A. N., V. C. Buttram, P. K. Besch, and R. G. Smith. 1979. Prolactin receptors in the ovary. Fertil. Steril. 31:273–277.

Rhodes, F. M., L. A. Fitzpatrick, K. W. Entwistle, and G. De'ath. 1995. Sequential changes in ovarian follicular dynamics in *Bos indicus* heifers before and after nutritional anoestrus. J. Reprod. Fertil. 104:41–49.

Richards, J. B., D. M. Hallford, and G. C. Duff. 1999. Serum luteinizing hormone, testosterone, and thyroxine and growth responses of ram lambs fed locoweed (*Oxytropis sericea*) and treated with vitamin E/selenium. Theriogenology 52:1055–1066.

Richards, M. W., L. J. Spicer, and R. P. Wettemann. 1995. Influence of diet and ambient temperature on bovine serum insulin-like growth factor-I and thyroxine: Relationships with non-esterified fatty acids, glucose, insulin, luteinizing hormone and progesterone. Anim. Reprod. Sci. 37:267–279.

Roberts, A. J., R. A. Nugent III, J. Klindt, and T. G. Jenkins. 1997. Circulating insulin-like growth factor I, insulin-like growth factor binding proteins, growth hormone, and resumption of estrus in postpartum cows subjected to dietary energy restriction. J. Anim. Sci. 75:1909–1917.

Saldarriaga, J. P., D. A. Cooper, J. A. Cartmill, J. F. Zuluaga, R. L. Stanko, and G. L. Williams. 2007. Ovarian, hormonal, and reproductive events associated with synchronization of ovulation and timed appointment breeding of *Bos indicus*-influenced cattle using intravaginal progesterone, gonadotropin-releasing hormone, and prostaglandin $F_{2\alpha}$. J. Anim. Sci. 85:151–162.

Schneider, F. A., and D. M. Hallford. 1996. Use of rapid progesterone radioimmunoassay to predict pregnancy and fetal numbers in ewes. Sheep Goat Res. J. 12:33–38.

Shibaya, M., S. Murakami, Y. Tatsukawa, D. J. Skarzynski, T. J. Acosta, and K. Okuda. 2006. Bovine corpus luteum is an extrapituitary site of prolactin production. Mol. Reprod. Dev. 73:512–519.

Short, R. E., R. A. Bellows, R. B. Staigmiller, J. G. Berardinelli, and E. E. Custer. 1990. Physiological mechanisms controlling anestrus and infertility in postpartum beef cattle. J. Anim. Sci. 68:799–816.

Slot, K. A., J. Kastelijn, A. Bachelot, P. A. Kelly, N. Binart, and K. J. Teerds. 2006. Reduced recruitment and survival of primordial and growing follicles in GH receptor-deficient mice. Reproduction 131:525–532.

Spicer, L. J., J. Alonso, and C. S. Chamberlain. 2001. Effects of thyroid hormones on bovine granulosa and thecal cell function in vitro: Dependence on insulin and gonadotropins. J. Dairy Sci. 84:1069–1076.

Spicer, L. J., and S. E. Echternkamp. 1995. The ovarian insulin and insulin-like growth factor system with an emphasis on domestic animals. Domest. Anim. Endocrinol. 12:223–245.

Spoon, R. A., and D. M. Hallford. 1989. Growth response, endocrine profiles and reproductive performance of fine-wool ewe lambs treated with ovine prolactin before breeding. Theriogenology 32:45–53.

Stevenson, J. S., S. K. Johnson, and G. A. Milliken. 2003. Symposium: Incidence of postpartum anestrus in suckled beef cattle: Treatments to induce estrus, ovulation, and conception. Prof. Anim. Sci. 19:124–134.

Tortonese, D. J., J. Brooks, P. M. Ingleton, and A. S. McNeilly. 1998. Detection of prolactin receptor gene expression in the sheep pituitary gland and visualization of the specific translation of the signal in gonadotrophs. Endocrinology 139:5215–5223.

Wagner, J. J., K. S. Lusby, J. W. Oltjen, J. Rakestraw, R. P. Wettemann, and L. E. Walters. 1988. Carcass composition in mature Hereford cows: Estimation and effect on daily metabolizable energy requirements during winter. J. Anim. Sci. 66:603–612.

Waterman, D. F., W. J. Silvia, R. W. Hemken, G. Heersche, T. S. Swenson, and R. G. Eggert. 1993. Effect of bovine somatotropin on reproductive function in lactating dairy cows. Theriogenology 40:1015–1028.

Wells, N. H., D. M. Hallford, and J. A. Hernandez. 2003. Serum thyroid hormones and reproductive characteristics of Rambouillet ewe lambs treated with propylthiouracil before puberty. Theriogenology 59:1403–1413.

Wettemann, R. P., and I. Bossis. 2000. Energy intake regulates ovarian function in beef cattle. Proc. Am. Soc. Anim. Sci. http://www.asas.org/JAS/symposia/proceedings/0934.pdf. Accessed May 15, 2007.

Wettemann, R. P., H. D. Hafs, L. A. Edgerton, and L. V. Swanson. 1972. Estradiol and progesterone in blood serum during the bovine estrous cycle. J. Anim. Sci. 34:1020–1024.

Wettemann, R. P., C. A. Lents, N. H. Ciccioli, F. J. White, and I. Rubio. 2003. Nutritional- and suckling-mediated anovulation in beef cows. J. Anim. Sci. 81(E. Suppl. 2):E48–E59.

Wise, T., and R. R. Maurer. 1994. Follicular development, oocyte viability and recovery in relation to follicular steroids, prolactin and glycosaminoglycans throughout the estrous period in superovulated heifers with a normal LH surge, no detectable LH surge, and progestin inhibition of LH surge. Domest. Anim. Endocrinol. 11:35–58.

Wright, I. A., S. M. Rhind, A. J. F. Russel, T. K. Whyte, A. J. McBean, and S. R. McMillen. 1987. Effects of body condition, food intake and temporary calf separation on the duration of the post-partum anoestrus period and associated LH, FSH and prolactin concentrations in beef cows. Anim. Prod. 45:395–402.